Catalogue of American Amphibians and Reptiles.

Ernst, C.H. and T.E.J. Leuteritz. 1999. *Geochelone denticulata*.

Geochelone denticulata (Linnaeus)
Yellow-footed Tortoise

Testudo denticulata Linnaeus 1766:352. Type locality, erroneously listed as "Virginia." Syntypes, two specimens (one a stuffed juvenile, the other shown in Schoepff 1792:plate 28, fig. 1) in the Museum de Geer; one of which was kept in Upsala and the other in Stockholm (Andersson 1900, Schoepff 1792). Anderson (1900) lists the holotype as NRM De Greer 21 (not examined by the author).

Testudo tabulatae Walbaum 1782:122. *Nomen illegitimum*, see **Comment**.

Testudo tessellata Schneider 1792:262. Type locality, not given. Type, not designated.

Testudo tabulata Schoepff 1793:56. Type locality, "In Africa australi?." Type, not designated. See **Comment.**

Testudo terrestris brasiliensis: Schweigger 1812:445. See **Comment.**

Testudo terrestris americana: Schweigger 1812:445. See **Comment**.

Testudo terrestris cayennensis: Schweigger 1812:445. See **Comment**.

Testudo terrestris surinamensis: Schweigger 1812:445. See **Comment**.

Testudo hercules Spix 1824:20. Type locality, "sylvis de flumen Solimoëns" [Rio Solimoes], Brazil. Holotype, an adult, now lost (Hoogmoed and Gruber 1983).

Testudo sculpta Spix 1824:21. Type locality, "sylvis juxta flumen Amazonum" [Rio Amazon], Brazil. Syntypes, originally five specimens in the Zoologische Staatssammlung München, of which four juveniles (2738/0, a shell; and 2753/0 A, B, C), fluid preserved specimens, are extant (Hoogmoed and Gruber 1983); Hoogmoed and Gruber (1983) designated 2753/0 A, the lectotype.

Testudo cagado Spix 1824:23. Type locality, "Cagado in campis et nemoribus campestribus Bahiae" [Salvador], Brazil. Holotype, an adult, now lost (Hoogmoed and Gruber 1983).

Testudo planata Gmelin, *in* Gray 1831:9. *Nomen nudum*.

Testudo foveolata Schinz 1833:40. *Nomen nudum*.

Geochelone (Chelonoidis) tabulata: Fitzinger 1835:122.

Geochelone (Geochelone) denticulata: Fitzinger 1835:122.

Testudo (Chelonoidis) denticulata: Williams 1950a:22.

Chelonoidis denticulata: Froes 1957:9.

Geochelone denticulata: Williams 1960:10. First use of present combination.

Geochelone (Chelonoidis) denticulata: Pritchard 1967:269.

Geochelone (Chelonoides) denticulata: Auffenberg 1971:110.

• **CONTENT.** *Geochelone denticulata* is a monotypic species.

• **DEFINITION.** *Geochelone denticulata* is the largest species of tortoise (to 82 cm straight carapace length) on the mainland of South America. It has an elongated carapace with a shallow cervical indentation. The lateral sides of the shell are parallel or slightly bowed, somewhat flared over the hind limbs, and with slightly scalloped posterior marginals and no cervical scute. Vertebrals are broader than long with the 1st and 5th laterally expanded. Adults have either weak or no growth rings on the vertebral and pleural scutes. Eleven marginals are usually present on each side, and the supracaudal is undivided and downturned. The carapace is brown with yellow to orange vertebral and pleural areolae; yellowish or orange pigment also occurs at the lower edge of each marginal. The plastron is well developed. Its upturned forelobe tapers toward the front and is about as long as, but slightly narrower than, the hindlobe, which bears an anal notch. The average plastral formula is: abd > hum > fem > gul >< pect >< an; the paired gulars are thickened, but do not extend much, if at all, beyond the carapacial rim. Each gular scute is longitudinally split on the dorsal side only. The bridge is long with a moderately sized axillary and a smaller inguinal that barely touches the femoral scute. The plastron is yellowish brown with darker pigment along the seams. The head is brown with yellow dorsal scales. It is moderate in size with a short snout and a slightly hooked upper jaw. The large prefrontal scale is divided medially and is followed by a subdivided frontal scale; other head scales are small, and yellow to orange with dark borders; the jaws are dark brown. The anterior surface of each forelimb is covered with large yellow or orange, non- or only slightly overlapping scales. No enlarged tubercles occur on the thighs, and the tail lacks a large terminal scale.

FIGURE 1. *Geochelone denticulata*. Photograph by Roger W. Barbour.

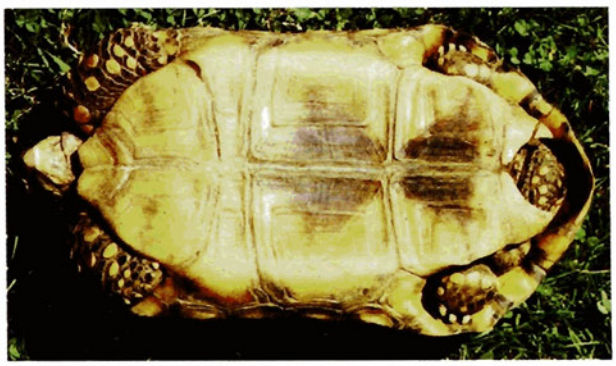
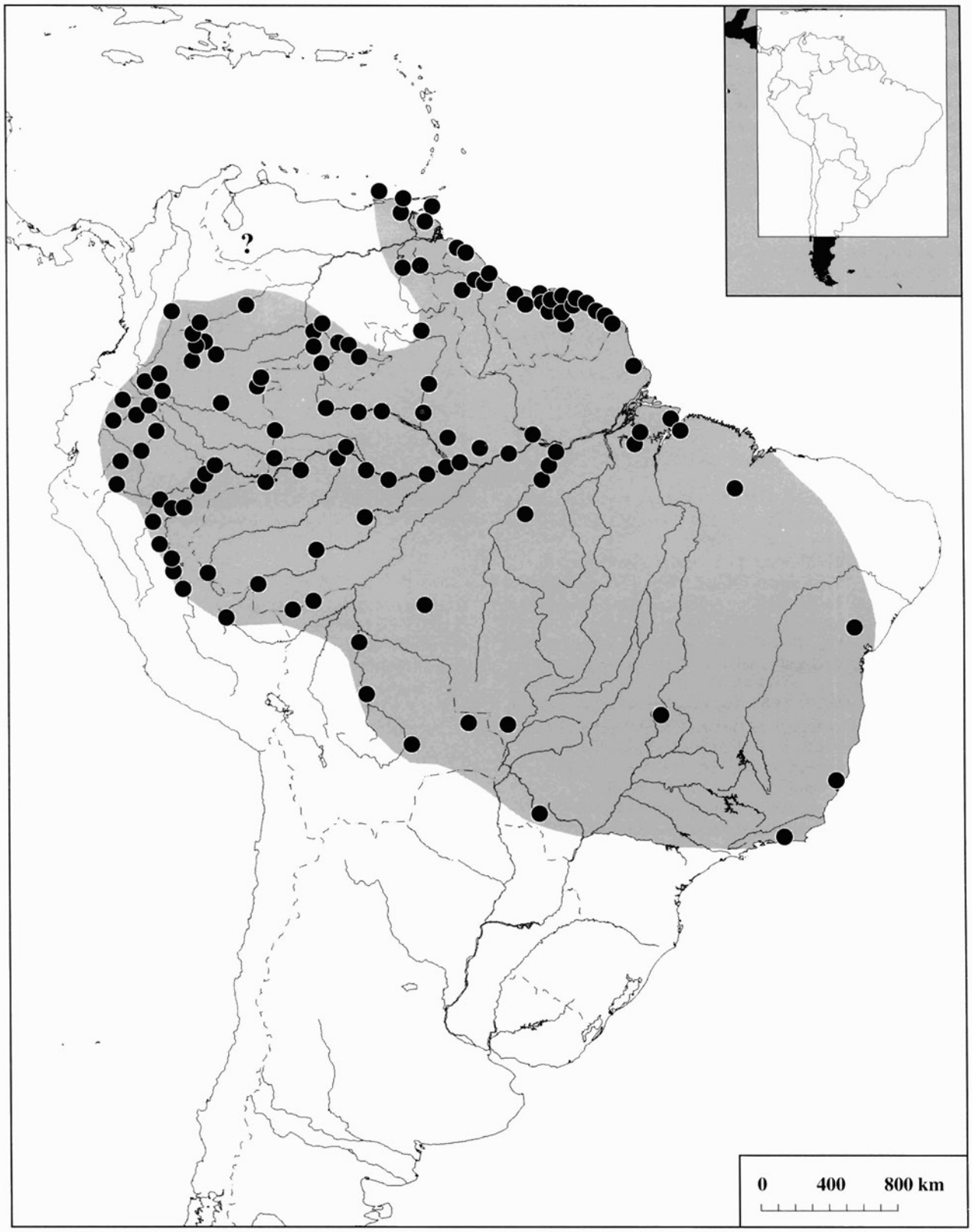


FIGURE 2. *Geochelone denticulata*, plastron. Photograph by Roger W. Barbour.

The karyotype is 2n = 52; 28 macrochromosomes (16 metacentric or submetacentric, 12 telocentric or subtelocentric) and 24 microchromosomes. It differs from that of *G. carbonaria* by centromere placement of one of the smallest macrochromosomes (Bickham and Baker 1976a, 1976b).

Adult males average slightly longer than females, but the females have greater average mass. Males have a concave plastron; carapace expanded over the hindlimbs; low, flattened, elongated profile; gular extensions that usually protrude beyond the anterior carapacial rim; and a longer, thicker tail. Females have a relatively domed, compact carapace; flat plastron; and a shorter gular and tail.

• **DESCRIPTIONS. Descriptions of adults** are in Auffenberg (1971), Boulenger (1889), Castaño-Mora and Lugo-Rugeles (1981), Ernst and Barbour (1989), Goeldi (1905), Gray (1855 [1856], 1870, 1873b), Hagan (1968), Luederwaldt (1926), Medem et al. (1979), Moreira (1991), Müller (1987), Müller and Hellmich (1936), Murphy (1997), Pritchard (1964, 1967, 1975, 1979), Pritchard and Trebbau (1984), Siebenrock (1909), and Williams (1960). **Juveniles** were described by Ernst and Barbour (1989) and Gray (1866). Descriptions of eggs are found in Snedigar and Rokosky (1950). Auffenberg (1966) described the **wrist and forehand bones**, Gray (1869, 1873a) various **skeletal features**, and Williams (1950b) the **central articula-**



MAP. Distribution of *Geochelone denticulata*. Dots indicate selected localities; the type locality (see Synonymy) cannot be plotted.

tions of the cervical vertebrae. **Sexual dimorphism** is described by Moskovits (1988).

• **ILLUSTRATIONS. Color illustrations of adults** are in Alderton (1988), Boos and Quesnal (1968), Métrailler and Le Gratiet (1996), Murphy (1997), Pritchard (1967, 1979), and Pritchard and Trebbau (1984). **Black and white illustrations of adults or the shell** are in Dowling (1961), Ernst and Barbour (1989), Hagan (1968), Métrailler and Le Gratiet (1996), Moreira (1991), Müller and Hellmich (1936), Oliver (1953), Pough et al. (1998), Paull (1983), Pritchard and Trebbau (1984), Snedigar and Rokosky (1950), Sowerby and Lear (1872), Spix (1824), Wermuth and Mertens (1961), and Williams (1960). **Juveniles or hatchlings** are illustrated in color or black and white in Calmonte (1968), Métrailler and Le Gratiet (1996), Pritchard and Trebbau (1984), Williams (1960), and a color photograph of **eggs** is in Pritchard and Trebbau (1984). **Sexually dimorphic characters** were shown by Snedigar and Rokosky (1950). **Head scalation** is presented in Hagan (1968), Métrailler and Le Gratiet (1996), Mlynarski (1959), and Williams (1960). The **skull** is illustrated in Auffenberg (1971), Wermuth and Mertens (1961), Gaffney (1979), and Ruckes (1937). Auffenberg (1966) illustrated the **wrist and forehand bones**, Gray (1873a, 1873b) showed the **plastral bones**, and Hoffmann (1882 [1883]) the **pelvic girdle**. The **karyotype** was illustrated by Bickham and Baker (1976b). Métrailler and Le Gratiet (1996) presented a color photograph of **habitat** and a black and white photograph of **copulation**.

• **DISTRIBUTION.** *Geochelone denticulata* is a denizen of tropical evergreen and deciduous rainforests. It ranges from southeastern Venezuela through the Atlantic lowlands of the Guianas to Brazil, where it occurs throughout the Amazon Basin to eastern Ecuador and Colombia, northern and eastern Perú, and northern and eastern Bolivia. It also occurs in an isolated range in eastern Brazil and on Trinidad. Accounts with data on distribution include: Ahrenfeldt (1954), Barbour (1934), Censky (1988), Cunha et al. (1985), Dixon and Soini (1977), Ernst and Barbour (1989), Grant and DeSola (1934), Hoge (1952), Iverson (1986, 1992), Legler (1963), Medem (1968), Medem et al. (1979), Menne (1954), Moreira (1989), Orces (1949), Pritchard (1967, 1975, 1979), Pritchard and Trebbau (1984), Roze (1964), Schmidt and Inger (1951) and Williams (1960). Distribution maps are in Iverson (1986, 1992), Métrailler and Le Gratiet (1996), Paull (1983), Pritchard (1975), Pritchard and Trebbau (1984), and Walker (1987, 1989).

• **FOSSIL RECORD.** No fossil of *Geochelone denticulata* has been reported.

• **PERTINANT LITERATURE.** *Geochelone carbonaria* (Spix 1824) was generally placed in the synonomy of *G. denticulata* (Linnaeus 1766) until Williams (1960) demonstrated that the two were different species. Consequently, the name *denticulata*, in literature prior to 1960, often represents a composite of the two taxa, making it difficult to determine which species is (are) involved unless illustrations are provided. The same is true of the names *Testudo tabulata* Schoepff 1793 and *T. tessellata* Schneider 1792.

Following are selected papers arranged by topic: **general accounts** (Alderton 1988; Boos and Quesnal 1968; Carillo de Espinoza 1970; Cunha et al. 1985; Ernst and Barbour 1989; Freiberg 1971, 1972; Fretey 1987; Goeldi 1905; Hernández 1971; Medem 1957; Menne 1954; Murphy 1997; Noel-Hume 1954; Paull 1983; Pritchard 1964, 1967, 1979; Pritchard and Trebbau 1984; Rodriquez-Bayona and Rylander 1984; Walker 1989), **evolution, systematics, and taxonomy** (Auffenberg 1971; Bour 1980; Castaño-Mora and Lugo-Rugeles 1981; Coto Rojas and Acuña Mesén 1986; Crumly 1988; David 1994; Hoogmoed and Gruber 1983; King 1989; Mertens and Wermuth 1955; Sullivan and Riggs 1967; Wermuth and Mertens 1961, 1977; Williams 1950a, 1952, 1960), **karyotype** (Bickham 1976; Bickham and Baker 1976a, 1976b; Dowler and Bickham 1982; Sampaio et al. 1971), **zoogeography** (Pritchard 1979), **size** (Sajdak and de Barros-Molina 1991), **longevity** (Dowling 1961, Oliver 1953), **cervical vertebrae** (Williams 1950b), **eye** (Underwood 1970), **head muscles** (Lakjer 1926), **thymus gland** (Bockman 1970, Van Bemmelen 1888), **parathyroid gland** (Van Bemmelen 1888), **rostral pores** (Winokur and Legler 1974), **mental glands** (Winokur and Legler 1975), **breathing** (Bellamy and Petersen 1968, Lenfant et al. 1970), **cutaneous gas exchange** (Jackson et al. 1976), **metabolism** (Benedict 1932), **serum proteins** (Newcomer and Crenshaw 1967), **hemoglobin** (Sullivan and Riggs 1967), **blood gases** (Rahn and Garey 1973), **blood buffering** (Lenfant et al. 1970, Rahn and Garey 1973), **sleep** (Monnier 1980, Walker and Berger 1972), **courtship** (Auffenberg 1964, 1965, 1977; Beltz 1954; Carpenter and Ferguson 1977; Pough et al. 1998; Snedigar and Rokosky 1950), **nesting** (Dixon and Soini 1977, Ehrenfeld 1979, Medem et al. 1979, Mowbray 1966, Pough et al. 1998, Snedigar and Rokosky 1950), **eggs** (Castaño-Mora 1985; Ewert 1979, 1985; Medem 1960; Medem et al. 1979; Moreira 1991; Mowbray 1966; Snedigar and Rokosky 1950; Watson 1969; Wilbur and Morin 1988), **hatchlings and juveniles** (Calmonte 1968, Medem et al. 1979, Watson 1969), **social behavior** (Auffenberg 1965, 1969, 1970, 1977; Beltz 1954; Carpenter and Ferguson 1977; Pough et al. 1998), **vocalizations** (Auffenberg 1964, 1965; Campbell and Evans 1967; Devertevil 1858), **habitat** (Auffenberg and Iverson 1979, Medem 1960, Obst 1986), **populations** (Moreira 1991, Moskovits 1988), **sex ratio** (Auffenberg and Iverson 1979), **diet and feeding behavior** (Beltz 1958, Bjorndal 1989, Derevtevil 1858, Ghilardi and Alho 1990 [1991], Highfield 1992, Hoge 1952, Moskovits and Bjorndal 1990, Moskovits and Kiester 1987), **predation** (Devertevil 1858, Emmons 1989, Pough et al. 1998), **swimming** Dixon and Soini 1977), **husbandry** (Calmonte 1970; Highfield 1992; Jakob 1970; Murphy and Collins 1983; Sims 1991a, 1991b), **parasites and disease** (Alho 1965, Beltz 1958, Costa et al. 1971, Díaz-Ungria and Gallardo Zerpa 1968, Fairchild et al. 1966, Hammerton 1939, Inglis and Díaz-Ungria 1963, Keymer 1978, Lainson et al. 1990, Rêgo 1967, Steck 1963, Walter 1990), and **common and vernacular names** (Froes 1957, Iverson 1985, Mittermeier et al. 1980).

• **ETYMOLOGY.** The name *denticulata* is a Latin derivative of *dens* (tooth), referring to the anterior and posterior carapacial rims which are very serrate in hatchlings and juveniles but only slightly so in adults.

• **COMMENT.** The species *Testudo denticulata* was described by Linnaeus (1766) on the basis of two specimens in the Museum de Geer (Andersson 1900). According to Williams (1960), Linnaeus' brief discription would not have been sufficient for identification if Schoepff (1792) had not published a color figure of a specimen that may have been one cited by Linnaeus and clearly was *denticulata*. Meanwhile, Walbaum (1782) proposed the name *Testudo tabulatae* for a brown and yellow tortoise referable to *denticulata*. This name, in its emendated form *tabulata* Schoepff 1792, became as popular as *denticulata*. Unfortunately, most early writers failed to recognize that the tortoise described as *Testudo carbonaria* by Spix (1824) was a legitimate species, including it within their concepts of *Testudo denticulata* or *T. tabulata*. This confusion of the status of the northern South American tortoises continued for a century until

Luederwalt (1926) suggested that two species were involved and Williams (1960) finally presented detailed evidence that *T. carbonaria* and *T. denticulata* are separate species. The name *Testudo tessellata* Schneider 1792 has also been used as a composite of *carbonaria* and *denticulata*, but is based on a description and figure which apply directly to *denticulata*.

The names *Testudo terrestris americana, T. t. brasiliensis, T. t. cayennensis*, and *T. t. surinamensis* Schweigger 1812 were based either on *Testudo terrestris* Fermin 1765 or *T. terrestris* Forsskål 1775. *Testudo terrestris* Fermin is both a suppressed senior subjective synonym of *Chelus fimbriatus* (Schneider 1783)(International Committee of Zoological Nomenclature 1963), and a *nomen oblitum* of *T. terrestris* Forsskål 1775, which was the earliest name applied to the European tortoise *Testudo terrestris*.

Pritchard (1986) critically diagnosed the original description of *Testudo gigantea* Schweigger 1812, and found no differences that would separate it from *Geochelone denticulata*, and thus thought the original description of *T. gigantea* was mistakenly based on a specimen of *G. denticulata*. Unfortunately, a holotype of *T. gigantea* was never designated, so this problem cannot be easily settled.

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